

## 8. CAPTURE-RECAPTURE METHODS.

### 8.1 Introduction

This chapter deals with some methods for estimating the absolute abundance of an animal population, using observations of marked individuals. There are two broad uses of marking for population studies. One use is in studying only the marked population with little attention paid to unmarked individuals. Such studies may be concerned with temporal movements (either local or migratory), delineation of geographic range ("home range" of individuals, range of particular population or sub-group of a population), or life history aspects (growth rates, survival rates, age specific reproductive rates, and so on). The other use is that of concern here, in which the primary interest is in the change in observed proportion tagged (which may initially be zero) as tagging progresses. The basic principle is the same in the change-in-ratio method. An important distinction is that the more complicated capture-recapture methods do make use of information as to the identity of single individuals. A distinction is made between "single-recapture" and "multiple-recapture" methods. In the early studies, the basic assumption for virtually all of the methods was that each and every individual in the population has the same probability of capture in any given sampling. Under such an assumption, any individual behaves like every other individual, and information that an individual has been caught once before or many times is largely irrelevant. One might equally well replace a marked individual with one from another population insofar as the theory of the method is concerned.

The assumption that individuals all behave alike insofar as capture is concerned is not very acceptable to most experienced field workers. In most cases, it is clear that the assumption is not realistic, and the issue is whether, in a given situation, the resulting bias can be tolerated. Various aspects of this problem will turn up in what follows. It is worth mentioning here, though, that one important means of testing the assumption of equal probability of capture does depend on the history of capture of individuals -- if individuals do not behave identically, then their past history gives information on that fact. In some models such information is used to produce an improved estimate of population size.

In describing the various methods, perhaps the most important aspect is that of whether the population is "open" or "closed" to those factors that may produce changes in the size of the population during the course of a capture-recapture study. Individuals may move into and out of the study areas, some may die, and others may be born or otherwise "recruited" to the population (in entomological studies, transfers between instars, pupation, etc., are additional such factors). A "closed" population with constant probability of capture permits very simple analyses, mostly based on the binomial distribution. Although such populations may not exist in practice, such a model provides a useful starting place, and may at times be adequate.

"Open" populations produce many more complications, particularly if they are small or if small changes are important. Then the models need to take into account chance effects, that is, stochastic (as opposed to deterministic) models need to be employed. Only quite recently have fully stochastic models been developed; fortunately their application in practice is less difficult than many of the previous methods. We are thus currently at a stage where only one general method may need to be considered in many practical situations. However, since that model also depends on the same unrealistic assumption of equal probability of capture, further

developments are needed, and the practicing ecologist will have to spend a great deal of effort in checking and cross-checking his estimates.

In some cases, the simpler methods may be adequate, or constitute about all that can be done under the circumstances of the study. Occasionally they may shed some light on particular aspects of a problem, or weakness in a necessary assumption that may not be apparent in the analysis of the more sophisticated form. Students will also need an understanding of the essentials of the various methods to understand and appreciate much of what they will find in the literature on a particular species. Thus a number of methods will be described here.

## 8.2 Petersen's method (Lincoln Index)

While the first recorded use of this method has been ascribed to Laplace in the 16th century (Cormack 1968), there are two commonly cited origins for its use in fish and wildlife work. Most fisheries workers know the technique as "Petersen's method" due to a suggestion by C.G.J. Petersen in 1896. Wildlife workers tend to refer to "Lincoln's Index" due to its use by F.C. Lincoln in efforts to estimate North American waterfowl abundance in the 1930's. A third early use was by C.H.N. Jackson (1933) in his studies of tsetse flies in Africa.

The method requires only two census periods, one involving the initial marking of  $M$  individuals, of which  $m$  are recovered in the  $n$  animals caught on the second occasion. If the population is closed (i.e., there are no gains or losses due to immigration, emigration, mortality, etc.), then it can be intuitively supposed that the fraction marked in the population ( $M/N$ ) may be estimated by the proportion of marked animals ( $m/n$ ) found in the second sample; that is:

$$m/n = M/N \quad \text{and} \quad \hat{N} = Mn/m \quad (8.1)$$

The relevant probability distribution is the hypergeometric distribution.

The assumptions necessary to the method can readily be understood by reference to the model resulting in a hypergeometric distribution. One description is via an "urn" model. Suppose we have a vessel of some sort (an "urn") containing  $N$  objects,  $M$  of which bear distinguishing marks (tags). If the objects are thoroughly mixed, one is removed and recorded (but not returned), then the remaining objects thoroughly mixed again, another removed and recorded, the objects mixed, another removed, and so on until  $n$  have been removed ( $m$  of which are marked), then the hypergeometric distribution serves to describe the behavior of the random variable  $m$ , the number of marked individuals recovered in a sample of  $n$ . In practice,  $n$  is also a random variable, but the usual approach is to consider the results to be "conditional" on the  $n$  actually observed, or to suppose that we sample on the second occasion until exactly  $n$  individuals are examined for marks.

One advantage of the urn model is that it helps clarify the position as regards random sampling. In the urn model there is no requirement that the  $M$  marks be put on according to any special scheme; the only requirement is thorough mixing before each draw (equivalent to random selection of the  $n$  animals taken on the second occasion). For all practical purposes, one thorough mixing is enough, so that one can infer the essential assumption to be one of either a random marking or a random recovery. Both are not required, as has been stated in the literature. In fact, it can be shown that the only essential feature is that the methods of capturing individuals need only be such that the individual probabilities of capture on the first occasion

are independent of those existing on the second (Junge 1963). Thus one might attempt to put tags on by, say, trapping and use another method (e.g., hunting) for recoveries. A difficulty with such an approach is in assuring that the two methods do in fact result in independence of the two sets of probabilities. This cannot be ascertained from two sampling periods alone. Another, less crucial, limitation is that the variance formulas (given below) do not apply unless capture probabilities are equal over all members of the population on the recapture occasion.

A summary of the assumptions is as follows:

- (1) The marks (tags) are not lost and are always identified on recapture.
- (2) The population is closed (but this assumption can be modified).
- (3) Every individual has the same probability of capture (at recovery time).

Assumption (2) can be modified in two ways:

(2a) There are losses of tagged and untagged animals which occur at the same rate, but there are no additions to the population. This does not change the proportion tagged and the estimate of population size remains valid but applies only to the population at the time of first sampling (tagging).

(2b) There are gains to the population between initial tagging and recovery of tags, but no losses, and the probability of capture is the same for all individuals during the recovery period. If there are no losses, then at the time of recovery, there are still  $M$  tagged individuals in the population, and the proportion tagged ( $m/n$ ) estimates what fraction of the current population carries tags, so that the estimate of eq.8.1 applies to the population at the time of recovery. Note that (2a) and (2b) thus estimate the population size at tagging and at recovery.

As we have already noted, assumption (3) can be modified as:

(3a) Marking at random.

(3b) Independent probabilities of capture at both marking and recapture (which necessarily includes (3a) as a special case).

These several modifications depart from the conditions necessary for the hypergeometric distribution to hold, and thus prevent strict applications of the relevant variance formulas. One simple way to obtain a useful estimate of the variance is to randomly subdivide the number of animals initially marked ( $M$ ) into several subgroups, and to estimate the population size separately for each such subgroup. These independent estimates then provide the data for calculating a valid variance. How many subgroups to use depends on the number marked initially ( $M$ ) and the fraction recovered, since there are obvious drawbacks in having any of the subgroups result in no recoveries of marked individuals. Presumably one might tolerate one such group, using the modified estimation formulas given below.

From a formal statistical point of view, the estimate of eq.(8.1) has the drawback of having an "infinite bias". This results because there is always a finite probability that  $m=0$  (i.e., no marked animals are caught on the second occasion). Chapman(1951) proposed an adjusted equation to circumvent this difficulty:

$$\hat{N}_C = \frac{(M+1)(n+1)}{(m+1)} - 1 \quad (8.2)$$

which has variance estimate:

$$v^* = \frac{(M+1)(n+1)(M-m)(n-m)}{(m+1)^2(m+2)} \quad (8.3)$$

When  $N$  is large, the hypergeometric distribution (sampling without replacement) is very closely approximated by a binomial distribution (sampling with replacement), and when  $P$  is sufficiently small, a Poisson distribution also provides an excellent approximation. On the other hand, when  $P$  is not very small, the normal distribution may provide an adequate model. Various rules have been suggested as to when to apply the several approximations in practice. Chapman(1948) used  $m/n$  as a guide to magnitude of  $P$ , and gave the following criteria:

$N < 500$	$m/n \leq .10$	Poisson
	$m/n > .10$	binomial
$500 < N < 1000$	$m/n \leq .075$	Poisson
	$m/n > .075$	normal
$1000 < N$	$m/n \leq .05$	Poisson
	$m/n > .05$	normal

However, other authors used less stringent rules. One of the best ways to gain insight into the differences due to various approximations is to intercompare sets of tables of the distributions for several examples.

The various approximations are particularly convenient in calculating a confidence interval around an estimate from the Petersen method. DeLury (1951) noted that, under the binomial assumption,  $P=M/N$ , so that the expected value of the random variable ( $m$ ) here representing the number of successes is:

$$E(m) = \frac{nM}{N} \quad (8.4)$$

with binomial variance:

$$V(m) = \frac{nM}{N} [1-(M/N)] \quad (8.5)$$

so that if we substitute  $m/n$  as an estimate of  $P$ , an estimate of the variance of  $m$  is just  $m[1-(m/n)]$ . Going one step further, and assuming  $m$  is approximately normally distributed, approximate 95 percent confidence limits for  $m$  are:

$$m \pm 2[m(1 - \frac{m}{n})]^{1/2}$$

and DeLury inserted these values in the Petersen estimate (eq.8.1) to provide confidence limits on  $N$ , i.e.,

$$\text{Upper limit} = \frac{nM}{\{m - 2[m(1 - m/n)]^{1/2}\}} \quad (8.6)$$

$$\text{Lower limit} = \frac{nM}{\{m + 2[m(1 - m/n)]^{1/2}\}}$$

An alternative way to proceed is to write the estimate (eq.8.1) as  $N = M/p$ , where  $p = m/n$ , and to use tables or graphs to find confidence limits on  $P$  in order to calculate upper and lower limits for  $N$  from those for  $p$ .

Still another approach (Leslie 1952) can be described by changing eqs. 8.4 and 8.5 from those representing the random variable  $m$ , to those for a random variable multiplied by a constant:

$$E(aX) = aE(X) \quad \text{and} \quad V(aX) = a^2V(X)$$

where  $a$  is a constant. If we use  $a = \frac{1}{nM}$ , then:

$$E\left(\frac{m}{nM}\right) = 1/N \quad (8.7)$$

$$V\left(\frac{m}{nM}\right) = \frac{1}{nNM} \left[1 - \frac{M}{N}\right]$$

but since  $N$  is unknown, we estimate the variance by replacing  $1/N$  by  $m/nM$  (eq.8.7 justifies this), and obtain:

$$s^2\left(\frac{m}{nM}\right) = \left[\frac{m}{(nM)^2}\right] \left[1 - \frac{m}{n}\right] \quad (8.8)$$

whereupon, assuming  $1/N$  to be approximately normally distributed, one can obtain approximate 95% confidence limits on  $1/N$  as:

$$\frac{1}{N} \pm 2 s\left(\frac{m}{nM}\right) \quad (8.9)$$

The main advantage here is that estimators of  $N$  are quite skewed as can be seen from sampling experiments, or by considering  $p (=m/n)$  to be normally distributed and reflecting what the distribution of  $1/p$  will look like. It turns out that  $1/N$  is much more symmetrically distributed, hence confidence limits expressed as in eq.(8.9) are presumably less biased than those previously described here.

Assuming a binomial distribution (rather than the hypergeometric) leads to a slightly different correction for bias in the estimation equations. Bailey (1952) suggested:

$$\hat{N}_B = \frac{M(n+1)}{(m+1)} \quad (8.10)$$

with variance estimate:

$$v_1 = \frac{M^2(n+1)(n-m)}{(m+1)^2(m+2)} \quad (8.11)$$

The difference between eq.(8.2) and eq.(8.10) is clearly very small. Bailey (1952) showed that  $N$  as estimated from eq.(8.1) tends to overestimate, having a bias "of order  $1/m$ ", while eq.(8.10) has a bias of order  $e^{-m}$ .

Cormack (1968:460) and Seber (1982) provide convenient summaries of a number of schemes to avoid biased estimates through "inverse" sampling. These schemes require sampling on a second occasion to continue until some pre-

determined event happens, e.g, until exactly  $m$  marked animals are caught. In many field situations such schemes are very difficult to carry out, and, as previously indicated here, the crucial source of bias is that having to do with unequal probabilities of capture, for which satisfactory corrections are presently difficult. In most practical situations, the investigator should use eqs. (8.2) or (8.10). If the numbers of recaptures ( $m$ ) is small enough to make the theoretical biases in estimation important, it will also be true that the estimates will be highly variable, and thus will provide very little information on the population under study in any case.

#### Example 8.1 Petersen method

Nixon et al. (1967) trapped and marked squirrels (Sciurus) in Ohio in 1962. In their first day of trapping, 22 individuals ( $M$ ) were caught, while on the second day, 13 were caught ( $n$ ). Seven of these were marked ( $m$ ), having also been caught on the first day. From eq. (8.1), we have:

$$\hat{N} = \frac{22(13)}{7} = 40.9, \text{ while Chapman's equation (8.2)}$$

gives:

$$\hat{N}_c = \frac{23(14)}{8} - 1 = 39.2, \text{ with variance estimate:}$$

$$v(\hat{N}_c) = \frac{23(14)(15)(6)}{64(9)} = 50.31$$

DeLury's estimated confidence limits are (eq. 8.6) calculated from:

$$\frac{13(22)}{7 \pm 2[7(1 - \frac{7}{13})]^{1/2}}$$

which gives:  $28.0 \leq N \leq 84.0$ . Leslie's approach (eq.8.8 and 8.9) gives:

$$s^2(\frac{nm}{M}) = \frac{7}{[13(22)]^2} (1 - \frac{7}{13}) = 0.0000395$$

and  $0.0119 \leq 1/N \leq 0.0370$  which is useful if one has some interest in the reciprocal of population size. Inverting gives essentially the same result as DeLury's approach. Bailey's method (eq. 8.10) gives:

$$\hat{N}_B = \frac{22(14)}{8} = 38.5 \text{ with variance estimate (eq. 8.11):}$$

$$s^2(\hat{N}_B) = \frac{(22)^2 14(6)}{64(9)} = 70.6.$$

### 8.3 The Schnabel method

We now consider a situation wherein sampling is not restricted to two occasions, and all of the unmarked animals caught in successive samples are marked and returned to the population. In most applications, the marks only serve to indicate that the animal has been caught previously and do not identify individuals. The

method was first proposed by Schnabel (1938) and further studied by Schumacher and Eschmeyer (1943) who provided a variance estimate and an alternative estimation formula (also derived by Hayne 1949). The basic assumptions are those previously given, i.e., (1) marks are not lost nor missed, (2) the population is closed, and (3) constant capture and recapture probabilities.

A very convenient way to visualize the process and to derive the various equations is that of DeLury (1958). An initial sample serves to introduce some marked individuals into the population, and then  $k$  further samples are taken (giving  $k+1$  sampling periods in all). Estimates are obtainable for population size in each of the subsequent sampling occasions but not for the first (although the assumptions do, of course, imply that the population is of constant size throughout the study). It is worth noting that there is no requirement that the first set of marks be put on at random (i.e., that all individuals have the same probability of capture). Thus if it is feasible to mark a substantial number of animals by some inexpensive but obviously biased method, the investigator might profitably do so, and then revert to some more expensive means of capture that is more in line with the assumptions for the  $k$  subsequent recapture periods.

The notation used here is as follows:

$M_i$  = number of marked individuals in the population just before the  $i^{\text{th}}$  sample is taken;  $i = 0, 1, 2, \dots, k$  so that  $M_0$  is the number marked on the first occasion.

$n_i$  = number of individuals caught on  $i^{\text{th}}$  sampling (since, in most studies,  $n_0 = M_1$ , we will be concerned here with  $n_1, n_2, \dots, n_k$ ).

$m_i$  = number of tagged individuals caught in the  $i^{\text{th}}$  sample;  $m_0 = 0$ , and we consider  $m_1, m_2, \dots, m_k$ .

In any given sampling (after the initial marking),  $m_i/n_i$  gives an estimate of the proportion marked in the population. If sampling is random with respect to whether or not the animal is marked (i.e., a constant probability of capture holds), then we have a binomial-type situation applying at the time of sampling, and we can write (with  $p = \frac{m_i}{n_i}$ ):

$$E\left[\frac{m_i}{n_i}\right] = \frac{M_i}{N_i} \quad (8.12)$$

$$V\left[\frac{m_i}{n_i}\right] = \frac{M_i}{N n_i} \left[1 - \frac{M_i}{N}\right] \quad (8.13)$$

Since  $N$  is unknown, it is necessary to use  $m_i/n_i$  to estimate the variance, as is usual in dealing with samples from a binomial distribution. The data from a capture-recapture study can be conveniently plotted with  $m_i/n_i$  on the vertical axis and  $M_i$  along the horizontal, and ideally should constitute a series of points ( $m_i/n_i$  and  $M_i$ ) scattered about a straight line through the origin. Solutions to the problem of estimating  $N$  depend on the choice of methods for fitting a regression line to the data. That is, eq.(8.12) can be represented as a straight line through the origin with slope

equal to  $1/N$ ; if one writes  $y_i = m_i/n_i$  and  $x_i = M_i$ , then the line  $y_i = bx_i$  is equivalent to eq. (8.12) with  $b = 1/N$ .

Since the "y" values ( $m_i/n_i$ ) are subject to sampling (chance) errors, a weighted regression scheme is indicated. One choice is to use reciprocals of the variance estimates [eq.(8.13)] as weights (thus the more precise data have greater weights). This procedure leads to Schnabel's original formula, which has to be solved by iterative (trial-and-error) methods; that is one finds a value of  $N$  most nearly satisfying:

$$\sum m_i = \sum \frac{(n_i - m_i)M_i}{\hat{N} - m_i} \quad (8.14)$$

for which Schnabel gave an approximate solution as:

$$\hat{N} = \frac{\sum n_i M_i}{\sum m_i} \quad (8.15)$$

However, DeLury pointed out that one of the common features of actual application of the method is that of a tendency for tagged individuals to be grouped or clustered in the habitat, which makes eq.8.13 a poor variance estimate (it underestimates). He therefore proposed weighting by the "sample size" ( $n_i$ ) at each point in time. This gives the simpler Schumacher-Eschmeyer formulation:

$$\hat{N} = \frac{\sum n_i M_i^2}{\sum m_i M_i} \quad (8.16)$$

A variance for the estimate (8.16) is calculated in the same manner as for weighted regression equations. This gives:

$$s^2 = \left\{ \sum \left( \frac{m_i^2}{n_i} \right) - \frac{(\sum m_i M_i)^2}{\sum n_i M_i^2} \right\} / (k-2) \quad (8.17)$$

and confidence limits are calculated from:

$$C.L. = \frac{\sum n_i M_i^2}{\sum m_i M_i \pm t_\alpha [s^2 \sum n_i M_i^2]^{1/2}} \quad (8.18)$$

where the  $\pm$  sign determines lower and upper limits respectively, and  $t_\alpha$  refers to the value obtained from t-tables for selected  $\alpha$  and  $k-2$  degrees of freedom. An important point here is that a small number of sampling times will result in fairly large values of  $t_\alpha$  and hence wider confidence limits than might be obtained with more days of tagging.



### Example 8.2 The Schnabel method

The trapping mentioned above (Example 8.1) was continued for a total of 11 days. The data are given below, along with the calculations for eq.(8.16).

Day	Number caught ( $n_i$ )	Recaptures ( $m_i$ )	Tagged in population ( $M_i$ )	$\Sigma m_i M_i$	$\Sigma n_i M_i^2$	$\hat{N}$
1	22	0	0	0		
2	13	7	22	154	6,292	40.9
3	15	10	28	434	18,052	41.6
4	10	5	33	599	28,942	48.3
5	6	5	38	789	37,606	47.7
6	5	3	39	906	45,211	49.9
7	15	10	41	1,316	70,426	53.5
8	11	6	46	1,592	93,702	58.9
9	18	8	51	2,000	140,520	70.3
10	8	7	61	2,427	170,288	70.2
11	16	10	62	3,047	231,792	76.1

Using DeLury's regression approach to the data, we let  $y_i = \frac{m_i}{n_i}$ ,  $x_i = M_i$ , and  $\beta = \frac{1}{N}$ . Thus eq. (8.12) becomes  $E(y_i) = \beta x_i$ , and a weighted equation using sample sizes ( $n_i$ ) as weights is:

$$\hat{\beta} = \frac{\Sigma w_i x_i y_i}{\Sigma w_i x_i^2} = \frac{\Sigma m_i M_i}{\Sigma n_i M_i^2} \quad \text{and this estimates the reciprocal of } N, \text{ hence}$$

eq.(8.16).

Calculating a variance estimate (eq. 8.17). we get:

$$s^2 = \frac{1}{9} \left[ 44.772 - \frac{(3,047)^2}{231792} \right] = 0.5243, \text{ and 95\% confidence limits for } \hat{N}, \text{ from}$$

eq. (8.18) are:

$$\frac{231792}{3047 + 2.26[(0.524)(231792)]^{1/2}} = \frac{231792}{3047 \pm 788.59} \text{ or } 60.4 \leq \hat{N} \leq 102.6$$

Since the last day's trapping turned up 6 unmarked squirrels, there were at least 68 ( $M_{11} = 62$  and 6 unmarked) in the population, so the lower limit should be 68. In the next hunting season, 41 squirrels were shot, of which 25 were marked. Using eq.(8.2), we have  $N_C = \frac{69(42)}{26} - 1 = 110.5$  which is appreciably above the upper limit. The authors felt that probabilities of capture were not constant, with some individuals being more likely to be recaptured.

### Example 8.3 Estimation from frequency of capture

In a situation like that of Example 8.1 and 8.2, where it appears that the population is being underestimated, the best cure no doubt is to identify the

faulty assumption and do something about it. This is not always as easy as it sounds. One way is to mark by one technique and recover by another, e.g., to tag by trapping and recover tags in hunting. However, this approach doesn't necessarily cure the problem (see, for example, Eberhardt et al. (1963:43-47), in which a particular model, the geometric distribution was postulated for recaptures). There is, of course, no assurance that this model should hold widely. Seber (1982:Ch.4) summarizes the theory and gives some other models that might be used. Eberhardt (1969) found that the geometric distribution did seem to fit a wide range of recapture data (40 sets on 10 species). An example of application of the method is available in the paper by Edwards and Eberhardt (1967). A series of taggings were carried out on a population of cottontail rabbits confined to a 40 acre pen in Ohio, in the fall of 1961. Data for a Schnabel census are set forth below.

<u>Date</u>	No. of captures $n_j$	Recaptures $m_j$	Tagged in Population $M_j$
Oct. 24	9	0	0
25	8	2	9
26	9	6	15
27	14	3	18
28	8	4	29
29	5	4	33
30	16	8	34
31	7	4	42
Nov. 1	9	3	45
2	3	2	51
3	8	7	52
4	14	5	53
5	2	1	62
6	5	0	63
7	11	5	68
8	0	0	74
9	5	5	74
10	9	7	74
Totals	142	66	76

Students should carry out the Schnabel calculations in order to gain familiarity with the method. Edwards and Eberhardt (1967:Table 3), using eq. 8.16, obtained a population estimate of 97 animals. The actual population in the pen was 135 rabbits, previously caught by drive-netting (to avoid previous experience with box-traps, which were used for the experimental study of capture-recapture methods), and introduced on October 19, and 29, 1961.

Frequencies of capture were:

<u>Number of times caught</u>	<u>Number of rabbits</u>	<u>Number of captures</u>
1	43	43
2	16	32
3	8	24
4	6	24
5	0	0
6	2	12
7	1	7
	<hr/> 76	<hr/> 142

The underlying model for the frequency distribution (geometric distribution) is a very simple one:

$$f(x) = pq^x \quad (x=0,1,2,\dots)$$

where  $q=1-p$ , and  $p$  is the probability that the animal will not be caught at all, i.e.,  $f(0) = p$ . Strictly speaking, the geometric distribution applies to a conceptually infinite series of trials, and can be at best an approximation to reality. Seber (1982:Ch. 4) can be consulted for various other theoretical difficulties and for the nature of the approximations on which the method rests. In the present instance, there were 18 trapping days and the maximum number of time any individual was caught was 7. In some situations, when the maximum number of captures approaches the number of capture occasions, an adjustment for truncation may be needed (the number of trapping occasions sets an upper limit on the possible number of recaptures). Seber (1982:172-174) gives a method for doing this and uses the data of Example 8.2 above to illustrate the method.

The essentials for estimation by the frequency of capture method are as follows:

$$\hat{q} = \frac{s-r}{s-1} \quad \text{and} \quad \hat{N} = \frac{r(s-1)}{s-r}$$

where  $r$  is the number of individuals that are caught  $s$  times. Referring to the data above, it may be seen that  $r = 76$  and  $s = 142$ . Estimates thus are:

$$\hat{q} = \frac{142-76}{141} = 0.468 \quad \text{and} \quad \hat{N} = \frac{76(141)}{142-76} = 162.4$$

In this instance, the method thus overestimates the known population. The estimates above can be used to set up a goodness of fit test by calculating expected numbers as:

$$E(n_x) = Npq^x \quad x=1,2,\dots$$

and introducing estimates of  $\hat{N}$  and  $\hat{q}$ . This yields the following results:

<u>Number of times caught</u>	<u>Original number of rabbits</u>	<u>Calculated number</u>
1	43	40.42
2	16	18.92
3	8	8.86
4	6	4.15
5	0	1.94
6	2	0.91
7	1	0.42
	<hr/> 76	<hr/> 75.62

These are obtained from  $Npq = 162.4(0.5319)(0.4681) = 40.43$  for the first entry,  $Npq^2 = 162.4(0.5319)(0.4681)^2 = 18.92$ , and so on (multiplying each successive entry by 0.4681). It can be seen that the data are fitted reasonably well. However, students should do a chi-square calculation to check this. In the present example, 135 rabbits were introduced into the pen, so we have  $135 - 76 = 59$  in the not-caught (0) category. The expected number is  $162.4(0.5319) = 86$ , which is substantially larger.

#### Example 8.4 Mean Petersen method

The Schnabel method depends on the population being closed (i.e., the same population of  $N$  individuals is present throughout the study). If this assumption is doubtful or disproven, then it is necessary to use a more complex method in which rates of loss (and/or gain) to the population are estimated. Before doing so, it may be worthwhile to consider a very simple approach, in which Petersen estimates are formed from successive entries in the table of data. That is, referring to the data of Example 8.2, the first 2 days can be used to obtain a Petersen estimate, then the results from day 2 and day 3 can be used, and so on. As noted in Sec. 8.2, the assumption of a closed population can be relaxed somewhat for a Petersen estimate (assumptions 2a and 2b), so that the sequence of Petersen estimates may be used to look for evidence of a trend in the population. If both gain and losses are taking place, the method isn't, strictly speaking, acceptable. However, if day to day changes aren't large, the overall average may be useful. This leads to the "mean Petersen" estimate proposed by Chapman (1952; see also Seber 1982:138).

Estimates are formed according to eq.8.2 and averaged:

$$\hat{N} = \frac{1}{k-1} \sum_{i=2}^k N_i \quad (\text{only } k-1 \text{ estimates can be obtained from } k$$

periods).

Variances can be estimated by averaging the estimates of eq. 8.3 as:

$$v_1(N) = \frac{1}{(k-1)^2} \sum_{i=1}^k v(N_i)$$

or as the variance of the individual estimates:

$$v_2(N) = \frac{1}{(k-1)(k-2)} \sum_{i=2}^k [N_i - \text{ave}(N_i)]^2$$

Students should perform the calculations using the data of Example 8.3.

#### 8.4 Methods for "open" populations

All populations are subject to change, so the methods described thus far are mostly useful under circumstances such that any change in population size is likely to be of minor importance. As we noted earlier, if there are only gains or losses, the Petersen method may give a valid estimate for one of the two sampling occasions. In general, however, one needs to have a method capable of taking into account temporal changes in populations.

Early workers largely dealt with open populations by assuming constant rates of gain or loss. When populations are large, such deterministic models can be quite satisfactory. However, even when a large population is being studied, it usually turns out that some aspects of the study will depend on small numbers, and thus introduce a stochastic element into the analysis. Consequently, a number of models have been developed that have both deterministic and stochastic elements. Some of these models are very complex and require cumbersome or intricate calculations. Versions of a fully stochastic model for open populations were published by G.M.Jolly (1965) and G.A.F.Seber (1965). Cormack (1968) suggested that, inasmuch as virtually identical results were obtained independently by Jolly and Seber, the technique should be called the Jolly-Seber method.

Some of the earliest efforts to deal with open populations arose from the pioneer studies of C.H.N.Jackson on tsetse fly populations in Africa (Jackson 1937,1939,1940,1948). He used two rather different schemes, one (the "positive method") depending on a single release of a large number of individuals followed by a series of samplings in which marked and unmarked individuals were tallied, but no further marking was done (however, marked individuals were released again after capture). In the second, "negative" method, marking was accomplished on a series of occasions but recaptures were tallied only in one final intensive sampling. The negative method uses the greater reduction in returns from the earlier releases (as compared to those from later releases) to estimate survival rates, which are in turn used to estimate the number of marked animals alive in the population at the time of the final large scale recapture sampling. An estimate of population size at the final sampling can thus be obtained from the Petersen formula, but  $M$  is now estimated rather than known exactly. Because any immigrants are reflected in the final sampling, it is not necessary to make special provision for measuring immigration (of course the rate of immigration is not estimated).

On the other hand, the positive method may be expected to measure dilution by immigrants since all of the marking is done in the initial survey. Thus the decrease in proportion marked in successive surveys should reflect the effect of immigration (or other sources of unmarked animals). Combining the two methods gives the necessary ingredients for a complete analysis, and this is what the more recently developed methods are designed to accomplish. Although direct use of the Jackson methods is not now recommended, it may happen that one of the two schemes may be useful in special circumstances -- for example, in Jackson's work unskilled assistants

were sometimes used to carry out marking on a broad scale. Bailey (1951,1952) gave improved estimates for Jackson's methods, while Chapman and Robson (1960) described methods to improve on his survival estimates.

A method ascribed to Fisher and Ford (1947) is mainly of historical interest by virtue of its use of a "trellis" diagram to classify recaptures on each day by the dates of release. The method thus uses data on all previous recaptures of individuals. No variance estimate was given. A detailed study by Leslie and Chitty (Leslie and Chitty 1951, Leslie 1952, and Leslie, Chitty, and Chitty 1953) developed a rather extensive approach to dealing with open populations. They assumed that, with small samples, observational data as to various classes (e.g., date last caught) can be represented as a multinomial distribution, and thereby produced a series of estimating equations. One problem is that the solutions are very difficult to obtain if there are a number of sampling periods.

It is intuitively evident that estimation of gains and losses from a population will require a minimum of three sampling periods. Thus "Bailey's triple catch" method (Bailey 1951, 1952) is of interest both as an illustration and a prospective method for either pilot studies or rapid estimates. The various items of data are as follows:

Period(i)	Time	Total captured	Total tagged and released	Marked individuals caught later
0	0		$s_0$	
1	$t_1$	$n_1$	$s_1$	$m_{01}$
2	$t_1 + t_2$	$n_2$		$m_{012}, m_{02}, m_{12}$

In the above table,  $m_{01}$  are those caught in the first time period and recaptured in the second. Some of these appear again in the third period and are labelled  $m_{012}$ . The estimates are:

$$N_1 = \frac{s_1 n_1 (m_{02} + m_{012})}{m_{01} m_{12}} \quad (8.19)$$

$$\hat{\lambda} = \exp(\hat{\beta} t_2) = \frac{m_{01} n_2}{n_1 (m_{02} + m_{012})} \quad (8.20)$$

$$\hat{\mu} = \exp(-\hat{\alpha} t_1) = \frac{s_1 (m_{02} + m_{012})}{s_0 m_{12}} \quad (8.21)$$

Variance estimates are:

$$v(\hat{N}_1) = \hat{N}_1^2 \left[ \frac{1}{m_{01}} + \frac{1}{m_{12}} + \frac{1}{m_{02} + m_{012}} - \frac{1}{n_1} \right] \quad (8.22)$$

$$v(\hat{\lambda}) = \hat{\lambda}^2 \left[ \frac{1}{m_{01}} + \frac{1}{m_{02} + m_{012}} - \frac{1}{n_1} - \frac{1}{n_2} \right] \quad (8.23)$$

$$v(\hat{\mu}) = \hat{\mu}^2 \left[ \frac{1}{m_{12}} + \frac{1}{m_{02} + m_{012}} \right] \quad (8.24)$$

Note that  $\exp(\beta_{t_2})$  estimates the gains to the population in the time interval ( $t_2$ ) between second and third captures ( $\beta$  is an instantaneous rate, while  $\exp(-\alpha_{t_1})$  measures losses in the first time interval ( $t_1$  between initial marking and the second sample (first recaptures). For the method to be strictly valid, it has to be assumed that rates of loss and gain are constant during the study period, so the important estimates are  $\beta$  and  $\alpha$ . With this arrangement, one avoids the necessity for having  $t_1 = t_2$ .

The fully stochastic (Seber-Jolly) models use some additional notation and, in common with many earlier models, require knowledge of the identity of individual animals, or at least the occasions on which individuals are marked, so that in many cases identification of individuals is practically essential. Additional symbols used are as follows:

$s_i$  = marked animals released on the  $i^{\text{th}}$  occasion (the  $s_i$  may be equal to the  $n_i$  if all unmarked animals are marked and no individuals are killed in handling or otherwise removed from consideration).

$r_i$  = the number of the  $s_i$  that are again caught before the study is concluded.

$z_i$  = number of individuals in the population that have been marked before the  $i^{\text{th}}$  period and are caught again after the  $i^{\text{th}}$  period but not during the  $i^{\text{th}}$  period (this then is a measure of the marked animals known to be present during the  $i^{\text{th}}$  period but not caught then).

The first estimate required is that of the number of marked individuals ( $M_i$ ) alive at the  $i^{\text{th}}$  period:

$$\hat{M}_i = \frac{z_i s_i}{r_i} + m_i \quad (i=1,2,\dots,k-1) \quad (8.25)$$

There are again  $k+1$  marking periods, the first (denoted by a subscript of zero) and the last ( $k$ ) for which there is not sufficient data to estimate  $M_i$ . The basis for eq.(8.24) can be seen intuitively by considering the fraction  $z_i/(M_i - m_i)$  -- this is the proportion of the marked animals alive at time  $i$  that are not caught then but are subsequently caught. Furthermore, out of the  $s_i$  released on the  $i^{\text{th}}$  occasion,  $r_i$  are caught later. If the animals behave alike (the key assumption of equality of capture probabilities, again), then clearly these two fractions should measure the same quantity; hence equating them gives:

$$\frac{z_i}{M_i - m_i} = \frac{r_i}{s_i}$$

and rearranging yields the estimate of  $M_i$  given in eq. 8.26. Perhaps it should be mentioned that  $m_i$  represents number of tagged animals in the catch ( $n_i$ ) at the  $i^{\text{th}}$  period, as it has in previous models. Also, we retain the assumptions that tags are neither lost nor misread, as well as that of equality of probability of capture among individuals on each occasion (however, this probability can change between occasions).

Population size on the  $i^{\text{th}}$  occasion is simply estimated by the Petersen method:

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i} \quad (i = 1, 2, \dots, k-1) \quad (8.26)$$

Again, estimates for the first and last periods are not available.

Survival between sampling occasions ( $\phi_i$ ) is estimated very simply from the data on  $M_i$ :

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i + s_i - m_i} \quad (i=0, 1, \dots, k-2) \quad (8.27)$$

The denominator is comprised of the  $\hat{M}_i$  animals estimated to be alive at the  $i^{\text{th}}$  trapping plus any newly marked animals actually released at that time ( $s_i - m_i$ ).

The number of animals coming into the population is estimated as:

$$\hat{\beta}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + s_i) \quad (i=1, 2, \dots, k-2) \quad (8.28)$$

and the logic of the estimate is evident from its structure. There are  $N_i$  animals in the population at the  $i^{\text{th}}$  sampling of which  $n_i - s_i$  are removed (i.e., the  $n_i$  caught minus any removals; often  $n_i = s_i$  and none are removed by the experimenter). A fraction  $\phi_i$  of these survive to the next period, so the equation estimates the number of "recruits" still alive at the  $i+1^{\text{st}}$  sampling.

A fifth estimate, that of the probability of capture at the  $i^{\text{th}}$  sampling is often useful:

$$p_i = \frac{n_i}{\hat{N}_i} \quad (8.29)$$

Again the logic is straightforward, and an equivalent estimate is  $p_i = m_i / M_i$ .

The variances of the several estimates are complicated, reflecting the complexity of the underlying theoretical development. Seber (1982:Chapter 5) gave a full treatment. A briefer version with simpler equations appears in the monograph by Pollock et al. (1990). They use corrections for small sample biases of the kind used in eq.(8.2). Most users will no doubt depend on a computer program to estimate variances. A number of programs are available, and the Wildlife Society maintains a Web Page with access to a variety of programs. The address is:

<http://fwie.fw.vt.edu/wsb/>

This page contains a link to the Colorado State University Department of Wildlife and Fisheries and Colorado Cooperative Unit Web Page which provides access to program MARK, currently one of the major programs for capture-recapture and survival estimation. The Appendix to the present course contains a program (JSMP) to do the main calculations and to bootstrap results.



### Example 8.5 the Jolly-Seber method

The main difficulty in applying this method lies in understanding and making an accurate tally for the basic tables from which the estimates are made. These procedures can best be understood by starting with Table 8.1, which is a tabulation of the history of capture for 56 Weddell seals. There were 5 sampling or census occasions. On the first ( $i=0$ ), 28 tags were put out. On the second ( $i=1$ ), 12 new animals were tagged, 11 on the third, and 5 on the fourth. None were tagged on the fifth census (but this quantity is not relevant to the estimates, anyhow)

The entries in each census column denote the history of a given animal. Thus, tag number 1 was caught initially, but never seen again, while numbers 11 and 12 showed up on every occasion. Number 30 was not tagged until the second census ( $i=1$ ) and was not seen on the fourth ( $i=3$ ), but showed up again on the fifth visit to the study areas.

The basic table of summary data is Table 8.2, in which the entries are the  $m_{hi}$ , which is defined as the number caught in the  $i^{\text{th}}$  sample that were last captured in the  $h^{\text{th}}$  sample. The top two rows contain basic data from the actual census trip. The first item is the  $n_i$ , total number of animals examined on each census. The second item contains the number of tagged animals that were released at that census. In many studies, all of the untagged animals would be tagged and released, so that  $s_i$ , the number of tagged animals released into the populations at each census would be equal to  $n_i$ . In the present example, this was not possible, so that of the 63 ( $n_0$ ) animals observed in the first census, only 28 ( $s_0$ ) were actually tagged.

The  $m_{hi}$  entries in the body of the table start with  $m_{01}$ , which is the number of the 28 animals tagged on the first visit ( $i=0$ ) that were found again on the second visit. The next entry in that row ( $m_{02}=2$ ), are those of the 28 tagged animals that did not show up until the third census ( $i=2$ ). The final entry ( $m_{04}=1$ ) is tag number 22, who was observed only in the first and last censuses. All of this data comes from the first 28 tag numbers.

The next row of the table of  $m_{hi}$  includes tagged animals last seen on the second census ( $h=1$ ) and then observed on the third, fourth or fifth census. This now brings in the data from tag numbers 29-40, as they were tagged in the second census. Totals of the table row entries constitute the  $r_h$ , the number of animals last captured on the  $h^{\text{th}}$  sample and then reobserved at some time in the future. The final column includes those animals initially tagged but not observed again (i.e., tag numbers 1,2,5,6, etc.). This number is not used in the calculations, but serves as a check, since  $r_h$  plus this number equals the number of tagged animals released in the appropriate census (e.g. the 28 of  $s_0$  equals  $17 + 11$ ).

The only really practical way to be sure of one's understanding of this procedure is to actually reconstruct the other table entries from Table 8.1.

A second table is usually prepared as a means of calculating the  $z_i$ . This is shown as Table 8.3, which shows the  $c_{hi}$ , those individuals caught in the  $i^{\text{th}}$  sample that were last caught in or before the  $h^{\text{th}}$  sample. Thus inspection of Table 8.1 shows that  $c_{02}=2$ , i.e., tag number 3 and 8 meet this criterion. We also have, as a further example, that  $c_{04}=1$ , since there is only one

individual (tag 22) caught in the first and last censuses only. The sum of the row entries give  $z_1$ ,  $z_2$ , and  $z_3$ . These totals should be checked by scanning the tables with the appropriate definition in mind. For example,  $z_2$  is the number of animals caught both before and after the 3<sup>rd</sup> census ( $i=2$ ). Hence, tag numbers 9,10,13,16,17,22,...,40 qualify (11 in all). One could, of course, just make such a tally directly and not bother with Table 8.3, but it is best to have the cross-check resulting from making the table and then a direct count. Logically, entries  $c_{01}$ ,  $c_{12}$ ,  $c_{23}$ , and  $c_{34}$  should be in the table, but these are just  $m_0$ ,  $m_1$ , and  $m_3$  and do not correspond with the definition of  $z_1$ , i.e., caught before and after but not in the  $i^{\text{th}}$  sample. Once the necessary ingredients are in hand, calculation of the estimates is straightforward from the definitions given in equations 8.25 to 8.29.

Table 8.1. History of capture for Jolly-Seber census.

Tag number	Census number				
	0	1	2	3	4
<u>Tags put out at first census</u>					
1	1	-	-	-	-
2	1	-	-	-	-
3	1	-	1	1	1
4	1	1	-	-	-
5	1	-	-	-	-
6	1	-	-	-	-
7	1	1	-	-	-
8	1	-	1	1	1
9	1	-	-	1	1
10	1	-	-	1	1
11	1	1	1	1	1
12	1	1	1	1	1
13	1	1	-	-	1
14	1	1	1	1	1
15	1	1	1	-	1
16	1	1	-	-	1
17	1	1	-	1	-
18	1	1	1	-	-
19	1	-	-	-	-
20	1	-	-	-	-
21	1	1	1	-	1
22	1	-	-	-	1
23	1	-	-	-	-
24	1	-	-	-	-
25	1	-	-	-	-
26	1	-	-	-	-
27	1	-	-	-	-
28	1	1	1	1	-
<hr/>					
<u>Tags put out at second census</u>					
29	-	1	1	1	1
30	-	1	1	-	1
31	-	1	1	-	-
32	-	1	-	-	-
33	-	1	-	-	-
34	-	1	-	-	1

35	-	1	-	-	-
36	-	1	-	1	1
37	-	1	-	1	-
38	-	1	-	1	1
39	-	1	1	1	1
40	-	1	-	-	1

---

Tags put out at third census

41	-	-	1	-	-
42	-	-	1	-	-
43	-	-	1	-	-
44	-	-	1	-	-
45	-	-	1	1	1
46	-	-	1	-	-
47	-	-	1	-	-
48	-	-	1	1	-
49	-	-	1	-	-
50	-	-	1	-	-
51	-	-	1	1	1

---

Tags put out at fourth census

52	-	-	-	1	1
53	-	-	-	1	1
54	-	-	-	1	-
55	-	-	-	1	-
56	-	-	-	1	-

---

Table 8.2. Tabulation of the  $m_{hi}$ , the number caught on the  $i^{\text{th}}$  sample last captured on the  $h^{\text{th}}$  sample.

i	1	2	3	4	5		
<hr/>							
$n_i$	63	43	41	42	58		number not
$s_i$	28	24	24	22	23		seen again
0	-	12	2	2	1	17	11
1	-	-	11	4	4	19	5
2	-	-	-	11	3	14	10
3	-	-	-	-	15	15	7
<hr/>							
$m_i$	0	12	13	17	23		

Table 8.3. Tabulation of  $c_{hi}$ , the number caught in the  $i^{\text{th}}$  sample last caught in or before the  $h^{\text{th}}$  sample.

	i					
h	1	2	3	4	5	Total
<hr/>						
	-	-	2	2	1	5 = $z_1$
1	-	-	-	6	5	11 = $z_2$
2	-	-	-	-	8	8 = $z_3$
3	-	-	-	-	-	

---

A program in the Appendix (JSMP) calculates these results, and is illustrated with the above data.

### 8.5 The Manly-Parr method.

The Jolly-Seber method has largely become the standard method for dealing with open populations. A method devised by Manly and Parr (1968) gives very much the same results, but has not been widely used. With the availability of computer programs for the Jolly-Seber method, the Manly-Parr approach may not receive much further attention. It does have the advantage of simplicity and is worth remembering inasmuch as estimates can be obtained with an ordinary calculator. One can thus explore a set of data with without needing reference or access to a computer. Tabulate the data in a matrix of zeros and ones with dates of observation as columns and records of individuals as rows. For every column (except the first and last) identify those individuals known to be in the population on that date by finding those that were seen before and after that date. Label this group as  $C_i$  where  $i = 2, 3, \dots, k-1$  (or  $1, 2, 3, \dots, k-1$  if you designate the first occasion as 0 as done in the Jolly-Seber notation). Now count the number of individuals that were actually observed on that occasion, and designate them as  $c_i$ . Then:

$$\hat{p}_i = \frac{k_i}{C_i} \quad (i = 2, 3, \dots, s-1) \quad (8.30)$$

estimates the probability of capture on the  $i$ th occasion, and the population present on that date is estimated as:

$$\hat{N}_i = \frac{C_i}{\hat{p}_i} \quad (i = 2, 3, \dots, s-1) \quad (8.31)$$

The following figure shows Jolly-Seber and Manly-Parr estimates for a number of sets of data from a capture-recapture study of Weddell seals in Antarctica, and shows that the two methods gave virtually identical results.

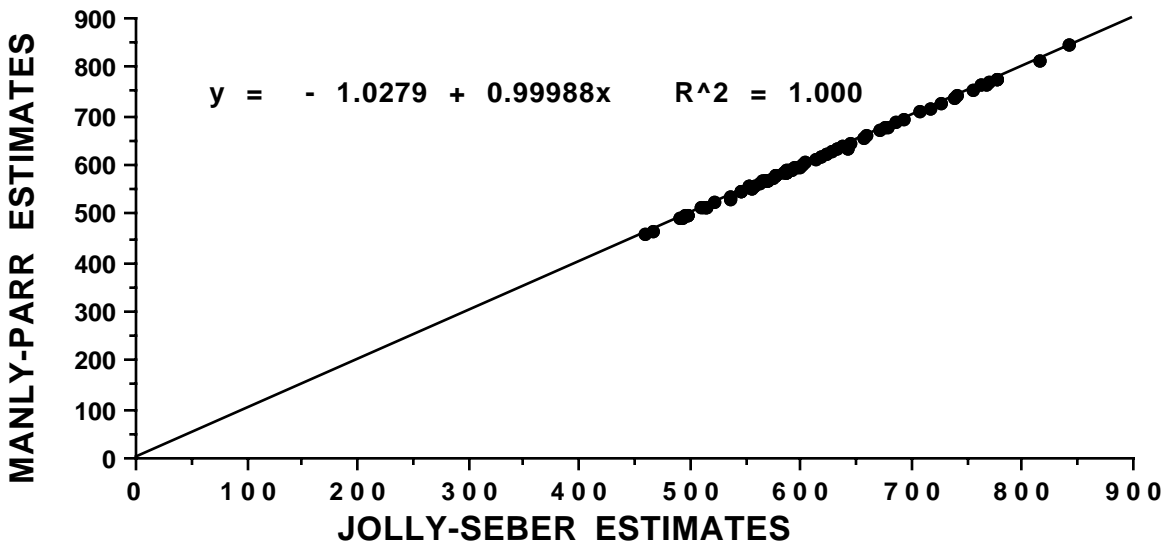


Fig. 8.1. Comparison of Manly-Parr and Jolly-Seber estimates for Weddell seal data.

A segment of data from that study appears below to illustrate the method.

DATE TAG NO.	1	2	3	4	5	6
727	1	0	1	0	0	0
748	1	0	1	1	1	0
818	1	1	1	1	1	1
1030	0	0	1	1	1	0
1040	1	1	1	1	1	1
1274	1	0	0	1	1	0
1286	1	1	1	0	1	1
1288	1	1	1	1	1	0
1445	0	0	1	0	1	0
1541	1	1	1	0	0	0
1577	1	1	0	0	0	0
1590	1	1	1	1	0	0
1594	1	1	1	1	0	1
1620	1	1	1	0	0	0
1893	1	1	1	1	1	0
1901	1	1	0	0	1	1
2018	1	1	1	1	1	0
2097	1	1	1	1	1	1
2285	1	1	1	1	1	1
2593	1	1	1	1	0	0
2619	1	1	1	1	0	0
2673	0	1	1	1	1	1
2700	0	0	1	1	1	1
2708	0	1	0	1	1	1
2717	1	1	1	1	1	1
2807	0	0	0	1	1	1
2930	1	1	1	1	1	0
2945	1	1	1	1	1	1
3010	1	1	1	1	1	1
3454	1	1	1	1	1	1
3511	1	1	1	1	1	0
3585	1	1	1	1	0	0
3685	1	1	1	1	1	1
3714	0	0	0	1	1	1
3923	1	1	1	1	1	1
3949	0	0	0	0	1	1
3999	1	1	0	1	1	1
4071	1	1	1	1	1	1
4190	0	1	1	1	1	0
4220	1	1	1	1	1	1
4224	1	1	1	1	1	1
$C_i$		31	31	30	22	
$c_i$		28	27	27	21	
$p_i$		0.903	0.871	0.90	0.954	

Because this is only a segment of the data, the results should not be taken as actual estimates of seal numbers.

The reason that the Jolly-Seber and Manly-Parr methods give essentially the same results, as suggested in Fig. 8.1, is that the equations for the proportion marked in the population actually converge to give identical values as the number of observations (i) increases. As discussed in Example 8.5 above, in some cases all unmarked individuals cannot be tagged at the time of capture, but instead “batch” tagging may be employed and an individual is treated as though it were newly tagged at the time of first capture. With this change, the main results and calculations are essentially the same, whether all newly caught individuals are tagged at capture, or only those carrying a tag from independent captures are considered as newly tagged. Convergence of the two methods can be shown most conveniently by starting with the estimate of the proportion tagged given below eq. (8.29):

$$p_i = \frac{m_i}{M_i} \quad (i = 2, 3, \dots, s-1) \quad (8.32)$$

introducing the estimate of the number marked in the population given by eq.(8.25), and rearranging to give:

$$p_i = \frac{1}{1 + \frac{R_i z_i}{m_i r_i}} = \frac{1}{1 + \frac{R_i (C_i - k_i)}{m_i r_i}} \quad (8.33)$$

This uses the evident fact that  $z_i = C_i - k_i$ . As i increases, the number of marked animals released ( $R_i$ ) eventually becomes equal to the number of marked animals encountered in the ith sample ( $m_i$ ) because there are no more initially marked animals that have not already been sighted for the first time. Similarly,  $k_i$  becomes equal to  $r_i$ , giving:

$$p_i = \frac{1}{1 + \frac{C_i - k_i}{k_i}} = \frac{k_i}{C_i} = \hat{p}_i$$

This then ultimately results in identical population estimates by the two methods for “batch” marking.

In the case of “batch” marking, the total population size is estimated by dividing the total number of animals seen (marked and unmarked) by the estimates of proportion seen [Eqs. (8.29) and (8.30)]. Comparisons of the two methods thus depend on eqs.(8.29) and (8.30), as the total number seen will be the same in both cases.

When marking of previously unmarked individuals continues throughout the study (“continued” marking), the Jolly-Seber method estimates total population size as Seber (1982, eq. (5.8,p.200):

$$N_i = \frac{M_i n_i}{m_i} \quad (i = 2, 3, \dots, s-1)$$

When there are no losses at capture, the number released is equal to the number seen, so:

$$N_i = R_i \left[ \frac{R_i z_i}{m_i r_i} + 1 \right] \quad (8.34)$$

For the Manly-Parr method with continued marking:

$$\hat{N}_i = \frac{R_i C_i}{k_i} \quad (8.35)$$

Again, as  $R_i$  approaches  $m_i$  and  $k_i$  approaches  $r_i$  with  $z_i = C_i - k_i$  we have equivalence of the two methods.

Example 8.6. Manly-Parr method.

Example 8.5 illustrated the Jolly-Seber method and the same data set is used here to demonstrate calculations for the Manly-Parr method.  $C_i$  and  $k_i$  are calculated just as illustrated above (page 8.21), with the data of Table 8.1 rearranged below in the same manner as on page 8.21.

1	1	0	0	0	0
2	1	0	0	0	0
3	1	0	1	1	1
4	1	1	0	0	0
5	1	0	0	0	0
6	1	0	0	0	0
7	1	1	0	0	0
8	1	0	1	1	1
9	1	0	0	1	1
10	1	0	0	1	1
11	1	1	1	1	1
12	1	1	1	1	1
13	1	1	0	0	1
14	1	1	1	1	1
15	1	1	1	0	1
16	1	1	0	0	1
17	1	1	0	1	0
18	1	1	1	0	0
19	1	0	0	0	0
20	1	0	0	0	0
21	1	1	1	0	1
22	1	0	0	0	1
23	1	0	0	0	0
24	1	0	0	0	0
25	1	0	0	0	0
26	1	0	0	0	0
27	1	0	0	0	0
28	1	1	1	1	0
29	0	1	1	1	1
30	0	1	1	0	1
31	0	1	1	0	0
32	0	1	0	0	0
33	0	1	0	0	0
34	0	1	0	0	1

35	0	1	0	0	0
36	0	1	0	1	1
37	0	1	0	1	0
38	0	1	0	1	1
39	0	1	1	1	1
40	0	1	0	0	1
41	0	0	1	0	0
42	0	0	1	0	0
43	0	0	1	0	0
44	0	0	1	0	0
45	0	0	1	1	1
46	0	0	1	0	0
47	0	0	1	0	0
48	0	0	1	1	0
49	0	0	1	0	0
50	0	0	1	0	0
51	0	0	1	1	1
52	0	0	0	1	1
53	0	0	0	1	1
54	0	0	0	1	0
55	0	0	0	1	0
56	0	0	0	1	0

Calculations for the above table:

C		15	22	21	
k		10	11	13	
n	63	43	41	42	58
p-tilde		0.667	0.500	0.619	
N-hat		64.5	82.0	67.8	

Here, p-tilde is calculated with eq.(8.30) and N-tilde uses eq. (8.31). A program (JSMP) to do the calculations is in the Appendix. It can be used for both the Jolly-Seber and Manly-Parr methods. A sequence longer than that of this example is required before the two sets of estimates converge. Even with this short sequence, the estimates are in fair agreement. Bootstrapping can be accomplished with the program, and the results for 1,000 bootstraps appear in the following table:

95% CONFIDENCE INTERVALS				
JOLLY SEBER				
i	2	3	4	
LOWER	48.2	63.5	51.5	
UPPER	107.5	214.9	114.4	
MANLY-PARR				
LOWER	47.8	58.6	51.9	
UPPER	103.2	143.5	105.0	
ORIGINAL DATA COMPARED TO BOOTSTRAP MEANS				
i	2	3	4	
JOLLY-SEBER				
N-hat	65.6	100.5	71.0	
BOOTSTRAP MEANS	68.2	109.9	74.0	
MANLY PARR				
N-tilde	64.5	82.0	67.8	
BOOTSTRAP MEANS	67.0	86.9	70.8	



The limited amount of data results in wide confidence limits, with only the upper estimates for the 3<sup>rd</sup> period being much different for the two methods, likely as a consequence of the different estimates for that period from the two methods.

For an example based on a much larger sample, some data on Hawaiian monk seals used by Eberhardt et al. (1999) have been processed with the same program. The results from the "Original data" worksheet follow:

	A	B	C	D	E	F	G	H	I	J	K	L
1	NROWS	C	k	R	m	r	n	M-hat	p-hat	p-tilde	N-hat	
2	225	70	35	81	35	81	83	70.00	0.5	0.5	166	
3	NCOLS	116	45	74	45	74	74	116.00	0.3879	0.3879	190.8	
4	20	145	56	79	56	78	81	146.14	0.3832	0.3862	211.4	
5		167	69	90	69	90	91	167.00	0.4132	0.4132	220.2	
6		188	63	80	63	80	80	188.00	0.3351	0.3351	238.7	
7		203	58	68	60	66	69	209.39	0.2865	0.2857	240.8	
8		207	77	84	81	80	84	217.50	0.3724	0.372	225.6	
9		210	67	67	67	67	67	210.00	0.319	0.319	210	
10		206	76	86	80	82	86	216.34	0.3698	0.3689	232.6	
11		203	81	92	90	83	92	225.23	0.3996	0.399	230.2	
12		204	87	88	88	87	89	206.34	0.4265	0.4265	208.7	
13		194	84	94	94	84	94	217.10	0.433	0.433	217.1	
14		184	74	84	84	74	85	208.86	0.4022	0.4022	211.4	
15		170	72	86	86	72	86	203.06	0.4235	0.4235	203.1	
16		157	58	71	71	58	71	192.19	0.3694	0.3694	192.2	
17		145	67	79	79	67	79	170.97	0.4621	0.4621	171	
18		134	71	82	82	71	82	154.76	0.5299	0.5299	154.8	
19		98	61	97	97.00	61	97	155.84	0.6224	0.6224	155.8	

Here we see that the estimates p-hat (Jolly-Seber) and p-tilde (Manly-Parr) are virtually identical. Bootstrapping (B =1,000) gave the results of Fig. 8.2.

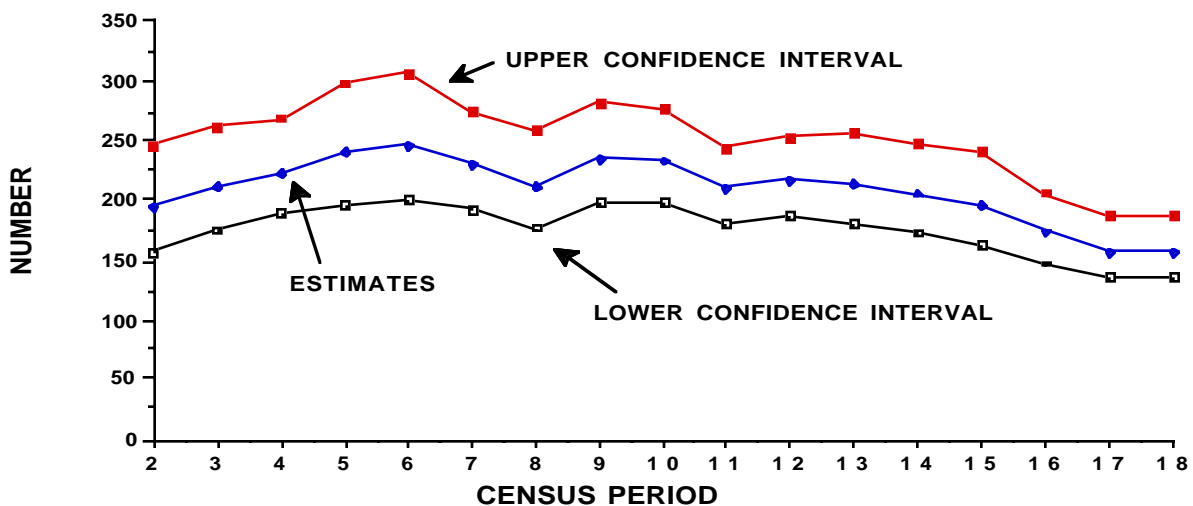


Figure 8.2. Bootstrap confidence limits for census data on Hawaiian monk seals collected on Laysan Island.

The "estimates" in Fig. 8.2 are actually the bootstrap means, but the actual estimates were virtually the same as the bootstrap means, being within 1 or 2 individuals. The original data for this site and for another (Lisianski Island) are on sheets attached to the program (JSMP) described and attached to the Appendix.

## 8.6. Tests of assumptions

As has been emphasized in previous sections, the crucial assumption in capture-recapture studies is that of equal probabilities of capture among the individuals comprising the population. Two major categories of failure of this essential assumption are:

- (1) The probability of capture inherently varies among individuals.
- (2) The probability of capture changes with exposure to the capture method.

The first class can be subdivided into two obvious groups, one being based on the frequent observation of behavioral differences between sex and age classes. This is a prospect most investigators will have in mind in designing a study, and one which can normally be dealt with by doing the necessary calculations for such groups separately. No doubt there will be other, more subtle, differences among individuals that will result in non-uniformity of response to the capture method, but, as with most features of free-living populations, such "second-order" differences can be neglected for many purposes.

The second sub-division of the first category constitutes the prospect of non-uniform application of the capture method. One of the most likely prospects is the occupancy of a "home-range" or "territory" by many terrestrial species. Unless the capture methods can be uniformly (or randomly) applied to the area under study on each sampling occasion, it is very likely that individuals will have rather different probabilities of capture. Live-trapping provides one example. If traps fall well within a heavily-used part of an individual's home range, clearly that individual can be expected to have a higher probability of capture than would be the case if the trap falls outside the periphery of the usual home range. One obvious precaution is to use a high density of traps relative to home range size; another is to move traps about during the study. Some work has been done on apparent effects of trap density, but very few efforts have been made to study the effect of shifting trapping patterns during the course of a study.

The second category is well-known, usually being labelled "trap-shyness" or "trap-proneness". Certainly there is little doubt that individuals of some species become very skilled at avoiding traps. Trap-proneness needs to be viewed with a little more caution. This is because a uniform probability of capture may nonetheless result in what appears to be an excessive number of captures for some individuals. More explicitly, with probability of capture  $P$  and  $n$  sampling periods, the probability that a given individual is caught  $x$  times follows the binomial distribution, which in turn, if  $P$  is small and  $n$  large, may be closely approximated by a Poisson distribution. Samples from a Poisson may well give the impression that some individuals are caught unduly often, that is, randomness usually doesn't look "random".

An immediate test to use on recapture data is to compare the frequencies with which individuals are captured with those expected under the hypothesis of a constant probability of capture: either a binomial or the corresponding Poisson

approximation. The simplest such test is the chi-square goodness of fit test. If there is evidence of appreciable gains to or losses from the population during the study then it is not appropriate to apply the test to all of the data. One must instead limit the test to a group of individuals known to be in the population during the period used. This means taking a set of individuals caught early in the study, and again before its conclusion. One thus has a group of individuals caught two or more times and known to be alive in some fixed time interval. Ideally, one would deal with a set of animals all caught on one of the first sampling periods, and then all caught again in the same period near conclusion of the study. In practice it may be necessary to group adjacent periods to obtain enough individuals to make the test worthwhile. An alternative test, suggested by Leslie(1958), is to apply the "binomial dispersion" test. This test compares the observed variability in frequencies of capture with that expected on theoretical grounds if the binomial distribution applies. Leslie(1958) suggested that at least 20 individuals should be available for the test, with 3 or more intervening recapture periods. Very likely the binomial dispersion test is to be preferred over the chi-square goodness of fit test.

Before applying any test to detect a violation of the underlying assumptions one needs to have a rather explicit notion as to what is being tested for, and what alternatives exist. Thus the above test assumes a constant probability of capture throughout the study, and may give an indication as to prospects for inherent differences in "catchability". Those problems associated with "trap-shyness" and its converse may be mainly associated with the first capture (or first few captures) and thus may not be detected in these tests. Also, if there are individuals in the population with essentially zero probability of capture, then no test based on recapture data can detect that problem (unless the true population size is known or otherwise estimated; even so very substantial numbers of recaptures may be required, see Cormack(1966)).

Various tests for the second category of violation of the basic assumption of constant probability of capture are given by Seber(1962,1965), Darroch(1958,1959), Leslie (1952), and Leslie, Chitty, and Chitty(1953). Little use seems to be made of these tests in practice, perhaps as a consequence of the complexity involved in their derivation and description. It is also unfortunately true that none of the tests are very "sensitive", i.e., they do not detect anything but extreme departures from equality of capture probabilities. The program "MARK" referenced in Section 8.4 above provides a wider range of tests, along with a criterion (AIC) for choosing among candidate models.

## 8.7 Exercises

8.71 Plot  $y(i)$  and  $x(i)$  of Example 8.2 and comment on validity of the underlying model.

8.7.2 Carry out the calculations for a Schnabel estimate on the data of Example 8.3. Plot  $y(i)$  and  $x(i)$  and comment on validity of the underlying model.

8.7.3 Do a chi-square calculation on the observed and expected frequencies of capture calculate in Example 8.3. The actual population in the pen was 135 rabbits giving  $135-76=59$  in the not-captured category. Use chi-square to check this against the expected number and comment on your results.

#### 8.7.4 Mean Petersen method.

Calculate the mean Petersen estimate described in Example 8.4 on the data of Example 8.3. Plot the data and compare with a plot of the Schnabel estimates obtained in Exercise 8.7.2. Discuss your results.

#### 8.7.5 Testing for constant probability of capture

In Example 8.2 (Schnabel), frequencies of capture were:

<u>Number of times caught</u>	<u>Number of squirrels</u>
1	33
2	16
3	10
4	4
5	2
6	3
	<hr/> 68

if the probability of capture is constant, these frequencies should be approximated by a Poisson distribution. Use a chi-square test to check the goodness of fit.

#### 8.7.6 Interpenetrating sampling

When animals are tagged in groups and tend to stay that way (i.e., clumped) until the recapture period, then it is essential that recaptures yield a random sample of the population, or at least that the probability of recapture not depend on whether or not a given individual is tagged. Sometimes this can be accomplished by taking a random sample of locations for recapture. If the recaptures come in groups, then eq.8.3, or any equation based on the assumption of random sampling of individuals, is not realistic. For an example of the bias that may result, students should refer to Example 4.8 and compare the variances obtained there with interpenetrating sampling with what would be obtained by combining all of the recaptures and using equation 8.3.

#### 8.7.7 Double-tagging

Tag loss can be a major source of bias in many circumstances. One way to improve the situation is to apply two tags to each individual. When this is done, then the probability of loss can be estimated from:

$$\hat{p} = \frac{m_s}{m_s + 2m_d} \quad \text{where } m_s \text{ and } m_d \text{ refer respectively to the number of}$$

recaptures carrying only one tag ( $m_s$ ) and retaining both tags ( $m_d$ ). A variance estimate is:

$$v(\hat{p}) = \hat{p}^2 (1 - \hat{p})^2 \left[ \frac{1}{m_s} + \frac{1}{m_d} \right]$$

and the appropriate Petersen estimate then becomes that of eq.8.1:

$$\hat{N}_d = \frac{Mn}{\tilde{m}} \quad \text{where } \tilde{m} = \frac{(m_s + 2m_d)^2}{4m_d}$$

with approximate variance:

$$v(\hat{N}_d) = \frac{\hat{N}_d^2}{\tilde{m}} \frac{\hat{p}}{(1 - \hat{p})^2} + \frac{\hat{N}_d^2}{\tilde{m}}$$

Data for calculations are taken from a fur seal double-tagging study (Abegglen et al. 1958), in which 34,923 male fur seal pups were single-tagged and 5,000 double-tagged on St. Paul Island off Alaska. In 1961, 48,458 three year old males were harvested, yielding the following returns:

2,098 originally single-tagged  
 258 double-tagged ( $m_d$ )  
 140 single-tagged ( $m_s$ )

Students should estimate: (1)  $\hat{p}$ , (2)  $v(\hat{p})$ , (3)  $\tilde{m}$ , (4)  $v(\hat{N})$ , and, (5) calculate an adjusted estimate from the single-tagging using  $\hat{p}$ , i.e.:

$$\hat{N}_{adj} = \frac{Mn}{\tilde{m}} (1 - \hat{p})$$

with variance:

$$v(\hat{N}_{adj}) = (1 - \hat{p})^2 v(\hat{N}) + \hat{N}^2 v(\hat{p})$$

### 8.7.8 Models for double-tagging

The underlying probability model for double-tagging is quite simple, and students should work out the basis for the above equations. Note that the probability of loss of each of the two tags is assumed to be the same. If the tags are of different kinds (or location, etc.) this assumption should be checked (with chi-square) and separate corrections may be required.

### 8.7.9 Survival estimation in a three-point census

The simplest census method for an open population requires observations on 3 occasions (an initial marking, a recapture period in which any unmarked are marked and a final capture period). Survival from tagging to the first recapture time is simply estimated as:

$$\hat{\Phi}_{01} = \frac{M_1}{M_0} \frac{m_{02}}{(m_{12} + 1)} \quad \text{with } v(\hat{\Phi}_{01}) = \hat{\Phi}_{01}^2 \left( \frac{1}{m_{02}} + \frac{1}{m_{12}} \right)$$

Data for southern hemisphere fin whales (17th report of International Whaling Commission) are:

Season	Number <u>marked*</u>	$m_{02}$	$m_{12}$	$\hat{\Phi}$
1953-1954	118	14	42	0.64
1954-1955	231	40	48	0.77
1955-1956	217	35	12	1.60
1956-1957	129	9	36	0.28
1957-1958	151	16	14	0.74
1958-1959	105	7	4	0.75
1959-1960	56	3	14	

\* Recoveries in the same season as the marking are not utilized.

Students should calculate  $\hat{\Phi}_{01}$  and the associated variance estimates, which might be compared with a variance calculated from the 7 estimates (which are not, however, independent).